

On the identity of the fossil aquatic beetles from the Tertiary localities in the southern part of the Upper Rhine Graben (Coleoptera, Hydrophilidae, Dytiscidae)

Martin Fikáček^{1,2}, Jiří Hájek¹, Heiko Schmied^{3,4}

1 Department of Entomology, National Museum, Kunratic 1, CZ-148 00 Praha 2, Czech Republic **2** Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic **3** Steinmann Institute of Geology, Mineralogy and Palaeontology, University of Bonn, Nüßallee 8, 53115 Bonn, Germany **4** Institute of Crop Science and Resource Conservation, Animal Ecology, University of Bonn, Melbweg 42, 53127 Bonn, Germany

Corresponding author: Martin Fikáček (mfikacek@gmail.com)

Academic editor: Jes Rust | Received 12 December 2010 | Accepted 25 January 2011 | Published 28 January 2011

Citation: Fikáček M, Hájek J, Schmied H (2011) On the identity of the fossil aquatic beetles from the Tertiary localities in the southern part of the Upper Rhine Graben (Coleoptera, Hydrophilidae, Dytiscidae). ZooKeys 78: 15–25. doi: 10.3897/zookeys.78.800

Abstract

This study focuses on the fossil beetles assigned previously to the family Hydrophilidae described from the localities in the southern part of the Upper Rhine Graben: Brunstatt (France, Alsace) and Kleinkems (Germany, Baden-Württemberg) (both dated ca. to Eocene-Oligocene boundary, 34 Ma). The identity of *Escheria convexa* Förster, 1891 is fixed by the designation of its neotype, the species is redescribed, illustrated, transferred from the hydrophilid genus *Hydrobius* Leach, 1815 to the genus *Copelatus* Erichson, 1832 (Coleoptera: Adephaga: Dytiscidae) and compared with other fossil representatives of *Copelatus*. The identity of the remaining three species, *Hydrobius crassipunctatus* (Förster, 1891), *H. dimidiatus* (Förster, 1891) and *H. punctulatus* (Förster, 1891), is briefly evaluated on the basis of the original descriptions and illustrations only, because their types were lost or destroyed during World War II; all three species are removed from the fossil record of the Hydrophiloidea and placed into Polyphaga *incertae sedis*. The geology and stratigraphy of Brunstatt and Kleinkems are discussed briefly.

Keywords

Dytiscidae, Hydrophilidae, *Copelatus*, *Hydrobius*, fossils, Eocene-Oligocene boundary, Brunstatt, Kleinkems, neotype designation

Introduction

In his study of the insects from the Tertiary outcrop of Brunstatt (Alsace, France), Förster (1891) described four species of the family Hydrophilidae, assigning all of them to the fossil genus *Escheria* Heer, 1847. Later, Théobald (1937) recorded two of these species from the locality of Kleinkems (spelled incorrectly as ‘Kleinkembs’ by the latter author), which is situated 16 km from Brunstatt and is believed to be of the same age and origin (see below for details). Based on the preserved characters, Théobald (1937) transferred all four of Förster’s (1891) species to the recent hydrophilid genus *Hydrobius* Leach, 1815. After 1937, the specimens were never re-examined and their identity remained unclear. Unfortunately, the Förster collection was either lost or destroyed during World War II (see Material and methods for details), which further complicates research.

For this study, we have re-examined the specimens from the locality of Kleinkems studied previously by Théobald (1937). In order to resolve the complicated situation concerning the four hydrophilid taxa, a neotype is designated for *Escheria convexa* Förster, 1891 and its taxonomic position is thus illuminated. The remaining fossils are excluded from the Hydrophiloidea due to the absence of any hydrophiloid apomorphy. Hence, our study supports the opinion by Fikáček et al. (2010) that various middle-sized Tertiary beetles were assigned into the hydrophilid genus *Hydrobius* irrespectively to their real taxonomic position.

Geology and stratigraphy of the fossil sites

The Tertiary outcrops of Brunstatt and Kleinkems were located in the south-west of central Europe and no longer exist today. Brunstatt was situated south of the city of Mulhouse in France (47°41'N 7°31'E); Kleinkems was situated in Germany (47°43'N 7°19'E) northwest of the city of Basel (Switzerland), about 16 km from Brunstatt. Several hundred fossils in total were collected at these localities (Wappler et al. 2005).

According to the reconstruction of the sedimentation history, the limnic sediments of Brunstatt and Kleinkems were deposited on the shore of a very large shallow saline lake (with an area of several hundred square kilometres) with episodic intrusion of fresh water (Lutz 1997). The landscape in this area originated during the formation of the Upper Rhine Graben (URG) which forms the central part of the Cenozoic Central European Rift System. Increased rifting during the late Middle Eocene to Early Oligocene led to the formation of the Mulhouse Potash Salt Basin (also called Potash Basin or Potassic Basin) which is located in the narrowest part of the graben and flanked by the highest of the Vosges Mountains and Black Forest Mountains (Hinsken et al.

2007). A detailed overview of the development of the URG and the Potash Basin is provided by Berger et al. (2005 a, b) and Hinsken et al. (2007).

Lutz (1997) and Mai (1995) assign the age of Brunstatt and Kleinkems to the Lower Oligocene, but Mai (1995) also allocated Brunstatt to the Mammal Reference Level MP20 which corresponds to the Priabonian (37.2–33.9 Ma) in the latest part of the Eocene. Thus, the stratigraphical position of Brunstatt and Kleinkems seems to be close to the Eocene-Oligocene boundary, as is the case of the similar fossil site of Altkirch in France (Wappler et al. 2005). According to Mai (1995) [based on Lakowitz (1895)], the palaeoclimate of Brunstatt was characterised by an average annual temperature of 18°C and abundant rainfall.

It seems very likely that the sediments of Brunstatt and nearby Kleinkems are nearly identical in age and genesis. Lutz (1995) even combined both localities in his study reconstructing their paleoenvironment, and according to Mai (1995), plant fossils from Brunstatt and Kleinkems are both deposited in the same layers of laminated clay ('plattiger Steinmergel').

Material and methods

Only the fossils from the locality of Kleinkems mentioned by Théobald (1937) deposited currently in the Naturhistorisches Museum in Basel, Switzerland (NHMB) were studied for this paper. The material originally examined by Förster (1891) was deposited at the 'Service de la Carte Geologique de Strasbourg' (Théobald 1937) and is considered to have been lost or destroyed during World War II on the basis of information we received from Jean Claude Horrenberger (École et Observatoire de la Terre, Strasbourg, France) as well as two letters sent to Volker Püthz, a specialist on Staphylinidae, by Marguerite Wolf (Université Louis Pasteur, Institut de Géologie, Strasbourg, France) in July 1967 and September 1971 (Püthz, pers. comm. 2010). The identity of species missing from the Kleinkems material is only discussed briefly on the basis of the original drawings by Förster (1891).

Fossils were examined using the Olympus SZ61 binocular microscope. Photographs were taken using the Canon MP-E 65 mm macro lens attached to the Canon EOS 550D camera. Drawings were traced from photographs. Abbreviations used in descriptions are: **EL** – length of the elytron; **TL** – total length, a single measurement of length from front of head to apex of elytra; **TL-h** – total length minus head length, length of body from anterior margin of pronotum to apex of elytra; **TW** – maximum width of body measured at right angles to TL.

Fossils whose family placement and hence also generic placement remains unclear are cited using the original combination of the name, placing the respective genus name in quotation marks.

Taxonomy

Coleoptera: Adephaga

Family Dytiscidae

Copelatus convexus (Förster, 1891) comb. n.

Figs 1–4

Escheria convexa Förster 1891: 359, plate XI, Figs 9a,b (original description from Brunstatt); Handlirsch 1908: 767 (catalogue).

Hydrobius convexus: Théobald 1937: 168, plate XII, Fig. 29 (transferred to *Hydrobius*, recorded from Kleinkems); Hansen (1999: 319, catalogue).

WWW site on Wikispecies. http://species.wikimedia.org/wiki/Copelatus_convexus

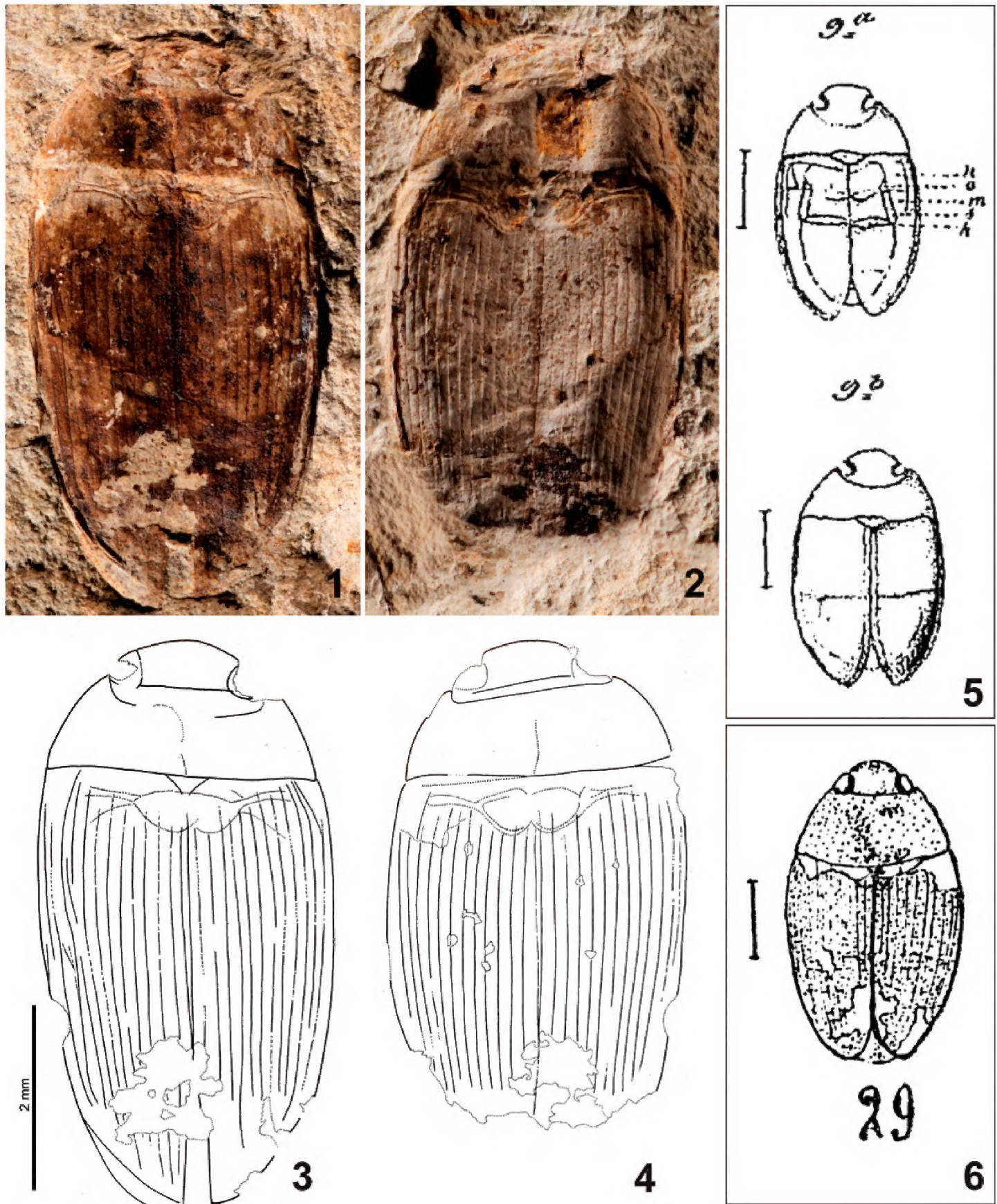
Material examined. Neotype, by present designation (NHMB): R91 (imprint) + R74 (counter-imprint) from the locality of Kleinkems (SW Germany, ca. Eocene-Oligocene boundary): fossil of the whole beetle in dorsal view, head, pronotum and elytra almost completely preserved; appendages missing.

Redescription. Body oblong-oval, broadest in basal third of elytra. Head relatively broad; compound eyes large, not exceeding body outline; clypeus rounded. Pronotum broadest between posterior angles, lateral margins regularly, moderately curved. Mesoscutellar shield well preserved, broadly triangular. Base of elytra as broad as pronotal base; lateral margins of elytra moderately curved. Only mesocoxae, part of metathoracic anepisternum, and probably part of apical abdominal ventrite perceptible from ventral part of body (Figs 1–4).

Surface sculpture. Pronotum with distinct longitudinal median impression, and poorly perceptible short longitudinal striae on disc. Elytra with 12 moderately impressed longitudinal striae.

Measurements. TL: 6.3 mm, TL-h: 5.6 mm, TW: 3.2 mm. EL: 5.2 mm.

Notes on the type material. The neotype corresponds well with the original description and drawings by Förster (1891) in the following characters: (i) general body shape; (ii) shape of the pronotum with projecting anterior angles; (iii) elytra with large number of longitudinal striae [preserved only in posterior portion of elytra in the holotype and their number is therefore estimated by Förster (1891) to be at least 10; 12 striae are present in the specimen from Kleinkems]; (iv) shape and proportion of the scutellar shield [much wider than long]; (v) body size [TL = 6.5 mm, EL = 4.3 mm, TW = 3.8 mm for the specimen from Brunstatt according to Förster (1891)]. The body proportions differ slightly between both specimens (the specimen from Brunstatt is relatively wider), but this may easily have been caused by deformation during the fossilization process or by the inaccuracy of the drawings by Förster (1891) which is quite usual for historic authors (e.g., compare the drawings by Théobald (1937) in Figs 6 and 12 with the actual appearance of the respective



Figures 1–6. *Copelatus convexus* (Förster, 1891). **1–4** neotype (**1, 3** NHMB R91; **2, 4** NHMB R74) **5** original illustrations of the holotype by Förster (1891) **6** drawing of the specimen NHMB R91 by Théobald (1937).

fossils). Moreover, Förster (1891) mentioned that his fossil resembles the dytiscid genus *Agabus* in most characters and did not assign it to the Dytiscidae merely because of its ventral morphology which was reconstructed by him as resembling that of *Polyphaga* (Fig. 5). It seems that Théobald (1937) examined Förster's types as he mentioned certain details which are absent in Förster's (1891) original publication,

and his opinion about the conspecificity therefore also has to be considered as a strong argument.

The reasons provided above together with the same age, geological origin and geographical proximity of both outcrops (Brunnstatt and Kleinkems) provide strong support for the conspecificity of both specimens mentioned by Théobald (1937). As the specimen from Brunstatt (i.e., the holotype) is lost, we consider it adequate to designate the specimen from Kleinkems as the neotype.

Generic attribution. The preserved characters of the ventral morphology, i.e. the narrow metathoracic anepisternum arising from the median coxal cavity and the anepisterno-metaventral suture directed lateroposteriad correspond closely with the ventral morphology of the Dytiscidae (see, e.g., Fig. 7.6.1 in Balke (2005)). The hydrodynamic body shape, large eyes, broad mesoscutellar shield, medium body size and distinct elytral striae enable us to classify the specimen without any doubt as belonging to the genus *Copelatus* Erichson, 1832 of the family Dytiscidae.

Copelatus is currently pantropical in its distribution and contains more than 400 described species (Nilsson 2001). Most species of *Copelatus* are characterised by longitudinal elytral striae whose number has been used to group the species into species groups (Sharp 1882); only a few species have smooth elytra (e.g., Hájek et al. 2010). Although the presence and number of elytral striae provides only limited evidence of phylogeny (Balke et al. 2004), the species groups delimited by number and position of elytral striae are frequently used as a tool for better orientation within the genus (e.g., Guignot 1961; Guéorguiev 1968; Nilsson et al. 1997). The European species previously classified in *Copelatus* have elytra without striae and have been transferred to the genus *Liopterus* Dejean, 1833 by Balke et al. (2004); they are not closely related to the fossil dealt with in this study.

Comparison with other *Copelatus* species. Altogether five species of fossil *Copelatus* species are known: *C. aphroditae* Balke, 2003 from Baltic amber (Eocene), *C. predaveterus* Miller, 2003 from Dominican amber (Miocene) (Miller and Balke 2003), and *C. fossilis* Říha, 1974, *C. ponomarenkoi* Říha, 1974 and *C. stavropolitanus* Říha, 1974 from the Miocene deposit of Stavropol (Říha 1974). The differences between all known species are summarized in Table 1.

Copelatus convexus differs from all known fossil and extant species of the genus in the presence of 12 longitudinal striae on each elytron. Sharp (1882) erected a group characterized by 12 discal striae (group 7) for a single species *Copelatus interruptus* Sharp, 1882 which is, however, currently classified in the genus *Exocelina* Broun, 1886 (Nilsson 2007). In contrast to the fossil *C. convexus*, this recent species has elytra with numerous short striolae rather than ‘true’ striae, see, e.g. Wewalka et al. (2010). Therefore, *C. convexus* might be provisionally classified in a separate *C. convexus*-group. However, it is necessary to point out that the counting of the precise number of lateral elytral striae is problematic in compressed fossils as the imprint of the submarginal stria may coincide with the lateral margin of the body or with the epipleuron. Therefore, we cannot rule out that a short submarginal stria was present in *C. convexus* although it is not perceptible in the fossil. In this case, *C. convexus* would belong to the *C. simoni*-group sensu Nilsson (2001).

Table 1. List of fossil species of the genus *Copelatus*, their basic morphological characteristics and their age. Body measurements in italics are estimated from usual TL/EL ratio in *Copelatus*.

Species	Period	Body length	Number of elytral striae	Species group (Nilsson 2001; Miller and Balke 2003)
<i>C. aphroditae</i>	Eocene	5.0 mm	19 discal	<i>C. aphroditae</i> -group
<i>C. convexus</i>	Eocene-Oligocene boundary	6.3–6.5 mm	12 discal	<i>C. convexus</i> -group
<i>C. fossilis</i>	Miocene	<i>6.1–6.5 mm</i>	10 discal + 1 submarginal	<i>C. erichsoni</i> -group
<i>C. ponomarenkoi</i>	Miocene	5.5–5.6 mm	6 discal + 1 submarginal	<i>C. irinus</i> -group
<i>C. predaveterus</i>	Miocene	3.8–4.4 mm	11 discal + 1 submarginal	<i>C. trilobatus</i> -group
<i>C. stavropolitanus</i>	Miocene	5.1 mm	11 discal	<i>C. nigrolineatus</i> -group

Coleoptera: Polyphaga

Family *incertae sedis*

‘Escheria’ crassipunctata Förster, 1891

Fig. 7

Escheria crassipunctata Förster 1891: 364, plate XI, Fig. 11 (original description from Brunstatt); Handlirsch 1908: 767 (catalogue).

Hydrobius crassipunctatus: Théobald 1937: 169, plate II, Fig. 28 (transferred to *Hydrobius*, referred from Kleinkems); Hansen 1999: 319 (catalogue).

Taxonomic notes. As in the case of *Copelatus convexus*, Théobald (1937) transferred *Escheria crassipunctata* to the hydrophilid genus *Hydrobius* and assigned fossil specimen no. R 707 from the locality of Kleinkems (deposited in NHMB) to this species. We have examined the specimen from Kleinkems for this study (Figs 10–11) but we cannot confirm that it is conspecific with *Escheria crassipunctata* for the following reasons: (i) the elytra are slightly constricted sub-basally in the specimen from Kleinkems, but evenly rounded laterally in *E. crassipunctata*; (ii) the body outline is distinctly interrupted between the pronotum and the elytra, but it is uninterrupted in *E. crassipunctata*, (iii) eyes are large and globular in the specimen from Kleinkems, but relatively small in *E. crassipunctata*. A more detailed comparison is impossible as the holotype of *E. crassipunctata* is lost and was moreover preserved in dorsal view based on the drawing by Förster (1891), whereas the specimen from Kleinkems is preserved in ventral view.

Based on the original drawing by Förster (1891), *Escheria crassipunctata* does not bear any synapomorphy of the Hydrophiloidea. For this reason, the species is removed from the fossil record of the Hydrophiloidea and is placed in Polyphaga *incertae sedis*.

Specimen no. R707 from Kleinkems does not bear any synapomorphy of the Hydrophiloidea, and moreover bears a combination of characters which excludes its assignment to the Hydrophiloidea: (i) prosternal process wide, (ii) mesocoxal cavities rather wide apart, and (iii) eyes large and globular. The preserved characters of this specimen do not allow an unambiguous family assignment (see Lawrence et al. 1999).

‘*Escheria*’ *dimidiata* Förster, 1891

Fig. 8

Escheria dimidiata Förster 1891: 363, plate XI, Figs 10a,b (original description from Brunstatt); Handlirsch 1908: 767 (catalogue)

Hydrobius dimidiatus: Théobald 1937: 169 (transferred to *Hydrobius*); Hansen 1999: 319 (catalogue).

Taxonomic note. Based on the original drawing by Förster (1891), the morphology of *Escheria dimidiata* agrees with that of Hydrophilidae: Hydrophilinae in many aspects: (i) mesocoxal cavities transverse, narrowly isolated from each other, (ii) metanepisternum rather narrow, (iii) epipleuron narrow but reaching elytral apex, and (iv) elytron with 10 longitudinal punctural series. None of these characters or their combination is, however, unique for the Hydrophiloidea and may be found in other beetle families as well (see e.g. Lawrence et al. 1999). Moreover, the medium body size (EL: 9 mm according to Förster (1891)) would indicate that the fossil should belong to the subtribes Hydrobiusina or Hydrophilina, whose representatives are characterized by a relatively large and well developed triangular mesoscutellar shield; in contrast, the scutellar shield is very small or reduced in *Escheria dimidiata*. Moreover, the re-examination of the fossil is impossible as the holotype was lost or destroyed. For all these reasons, *Escheria dimidiata* is removed from the fossil record of the Hydrophiloidea and is placed in Polyphaga *incertae sedis*.

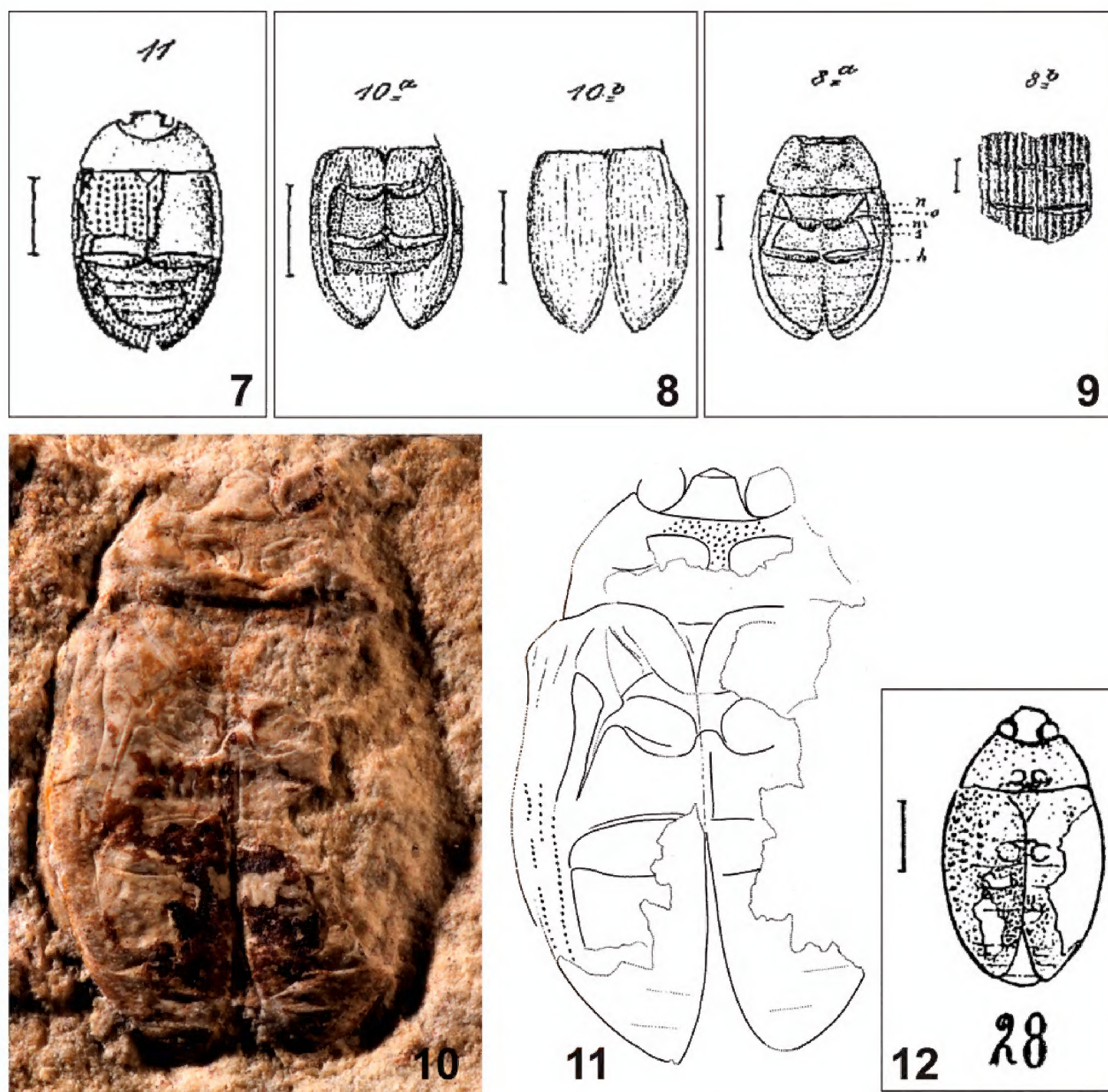
‘*Escheria*’ *punctulata* Förster, 1891

Fig. 9

Escheria punctulata Förster 1891: 361; plate XI, Figs 8a,b (original description from Brunstatt); Handlirsch 1908: 767 (catalogue).

Hydrobius punctulatus: Théobald 1937: 169 (transferred to *Hydrobius*); Hansen 1999: 319 (catalogue).

Taxonomic note. Based on the drawing by Förster (1891), the ventral morphology of this species agrees with that of Hydrophilidae: Hydrophilinae in many characters: (i) mesocoxae transverse and very narrowly separated, (ii) mesepimeron well separated, triangular, (iii) metanepisternum rather narrow; (iv) abdomen with five ventrites.



Figures 7–12. 7 '*Escheria*' *crassipunctata* Förster, 1891, original illustration of the holotype 8 '*Escheria*' *dimidiata* Förster, 1891, original illustration of the holotype 9 '*Escheria*' *punctulata* Förster, 1891, original illustration of the holotype 10–12 specimen NHMB R707 (10 photograph 11 drawing 12 original drawing by Théobald (1937)).

However, none of these characters or their combination is unique for the Hydrophiloidea and may be found in other beetle families as well (see Lawrence et al. 1999). Moreover, two characters illustrated on the drawing and/or mentioned in the original description exclude the placement of *E. punctulata* in the Hydrophiloidea: (i) elytra bear only 6 deeply impressed striae [9–11 striae are present in all Hydrophiloidea with striate elytra, only rarely is the number of series higher but in such cases they are never impressed to striae]; (ii) mesoventrite fused with mesepisternal (i.e. not separated from them by sutures) [in Hydrophiloidea, the mesoventrite is fused to mesepisterna only in derived groups of the Sphaeridiinae which are characterized by a highly elevated median portion of the mesoventrite; the elevated median elevation is missing from the fossil]. For these reasons, *Escheria punctulata* is removed from the fossil record of

the Hydrophiloidea and is placed into Polyphaga *incertae sedis*; its family placement remains unclear.

Acknowledgements

We are indebted to W. Etter (Naturhistorisches Museum, Basel) for the opportunity to re-examine the specimens studied by Théobald (1937), to J. C. Horrenberger (École et Observatoire de la Terre, Strasbourg) and V. Püthz (Max-Planck-Institut für Limnologie, Schlitz/Hessen) for information about the type specimens by Förster (1891), to T. Wappler (University of Bonn) for help with geological and paleontological literature, and to M. Lambertz and C. Carrington for proof reading the English text.

The study was supported by grant KJB301110901 from the Czech Academy of Sciences (GA AV), grant MK 00002327201 from the Ministry of Culture of the Czech Republic and grant MSM 0021620828 from the Ministry of Education of the Czech Republic.

References

- Balke M (2005) Dytiscidae Leach, 1915. In: Beutel RG, Leschen RAB (Eds) Handbook of zoology. A natural history of the phyla of the animal kingdom. Volume IV. Arthropoda: Insecta. Part 38. Coleoptera, Beetles. Volume 1: Morphology and systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim.). Walter de Gruyter, Berlin-New York, 90–116.
- Balke M, Ribera I, Vogler AP (2004) MtDNA phylogeny and biogeography of Copelatinae, a highly diverse group of tropical diving beetles (Dytiscidae). *Molecular Phylogenetics and Evolution* 32: 866–880.
- Berger JP, Reichenbacher B, Becker D, Grimm M, Grimm K, Picot L, Storni A, Pirkenseer C, Derer C, Schaefer A (2005a) Paleogeography of the Upper Rhine Graben (URG) and the Swiss Molasse Basin (SMB) from Eocene to Pliocene. *International Journal of Earth Sciences* 94: 697–710.
- Berger JP, Reichenbacher B, Becker D, Grimm M, Grimm K, Picot L, Storni A, Pirkenseer C, Schaefer A (2005b) Eocene-Pliocene time scale and stratigraphy of the Upper Rhine Graben (URG) and the Swiss Molasse Basin (SMB). *International Journal of Earth Sciences* 95: 711–731.
- Fikáček M, Prokop J, Nel A (2010) Fossil water scavenger beetles of the subtribe Hydrobiusina (Coleoptera: Hydrophilidae) from the Late Oligocene locality of Aix-en-Provence (France). *Acta Entomologica Musei Nationalis Pragae* 50: 445–458.
- Förster B (1891) Die Insekten des „Plattigen Steinmergels“ von Brunnstatt. *Abhandlungen zur geologischen Spezialkarte von Elsass-Lothringen* 5: 333–594.
- Guéorguiev VB (1968) Essai de classification des coléoptères Dytiscidae. I. Tribus Copelatini (Colymbetinae). *Izvestiya na Zoologicheskiya Institut s Muzey (Sofia)* 28: 5–45.

- Guignot F (1961) Revision des hydrocanthares d'Afrique (Coleoptera Dytiscoidea). 3. Annales du Musée Royal du Congo Belge, Série 8vo (Sciences Zoologiques) 90: 659–995.
- Hájek J, Hendrich L, Hawlitschek O, Balke M (2010) *Copelatus sibelaemontis* sp. nov. from the Moluccas, delineated based on morphology and DNA sequence data (Coleoptera: Dytiscidae). *Acta Entomologica Musei Nationalis Pragae* 50: 437–443.
- Handlirsch A (1908) Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Wilhelm Engelmann, Leipzig, 1430 pp. + 51 plates.
- Hansen M (1999) World Catalogue of Insects. Volume 2. Hydrophiloidea (s.str.) (Coleoptera). Apollo Books, Stenstrup, 416 pp.
- Hinsken S, Ustaszewski K, Wetzel A (2007) Graben width controlling syn-rift sedimentation: the Palaeogene southern Upper Rhine Graben as an example. *International Journal of Earth Sciences* 96: 979–1002.
- Lakowitz C (1895) Die Oligozänflora der Umgebung von Mühlhausen im Elsass. *Abhandlungen zur geologischen Spezialkarte von Elsass-Lothringen* 5: 180–360.
- Lawrence JF, Dallwitz MJ, Hastings AM, Paine TA (1999) Beetles of the world. A key and information system for families and subfamilies. CD-ROM, Version 1.0 for MS-Windows, Melbourne, CSIRO Publishing.
- Lutz H (1997) Taphozönosen terrestrischer Insekten in aquatischen Sedimenten – ein Beitrag zur Rekonstruktion des Paläoenvironments. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 203: 173–210.
- Mai DH (1995) Tertiäre Vegetationsgeschichte Europas. Fischer, Jena, 691 pp.
- Miller K, Balke M. (2003) The unusual occurrence of aquatic beetles in amber, *Copelatus aphroditae* Balke, n. sp. and *C. predaveterus* Miller, n. sp., (Coleoptera: Dytiscidae: Copelatinae). *Proceedings of the Entomological Society of Washington* 105: 809–815.
- Nilsson AN (2001) Dytiscidae (Coleoptera). *World Catalogue of Insects* 3: 1–395.
- Nilsson AN (2007) *Exocelina* Broun, 1886 is the valid name of *Papuadytes* Balke, 1998. *Latis-simus* 23: 33–34.
- Nilsson AN, Bilardo A, Rocchi S (1997) A check list of *Copelatus* Erichson 1832 species (Coleoptera Dytiscidae) from Afrotropical and Madagascan regions with a review of published penis drawings. *Tropical Zoology* 10: 11–48.
- Říha P (1974) Neue fossile Schwimmkäfer aus dem Tertiär Europas und Westsibiriens (Coleoptera, Dytiscidae). *Acta Entomologica Bohemoslovaca* 71: 398–413.
- Sharp D (1882) On aquatic carnivorous Coleoptera or Dytiscidae. *Scientific Transactions of the Royal Dublin Society, Series 2*, 2: 179–1003 + pls. 7–18.
- Théobald N (1937) Les insectes fossiles des terrains oligocènes de France. G. Thomas, Nancy, 473 pp.
- Wappler T, Hinsken S, Brocks JJ, Wetzel A, Meyer CA (2005) A fossil sawfly of the genus *Athalia* (Hymenoptera: Tenthredinidae) from the Eocene–Oligocene boundary of Altkirch, France. *Comptes Rendus Palevol* 4: 7–16.
- Wewalka G, Balke M, Hendrich L (2010) Dytiscidae: Copelatinae (Coleoptera). In: Jäch MA, Balke M (Eds) Water beetles of New Caledonia, part 1. *Monographs on Coleoptera* 3: 45–128.